Densities of *Penaeus aztecus, Penaeus setiferus,* and Other Natant Macrofauna in a Texas Salt Marsh

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ABSTRACT: Habitat-related densities of natant macrofauna were compared between vegetated and nonvegetated areas in a *Spartina alterniflora* marsh on Galveston Island, Texas. The most abundant macrofauna were crustaceans, *Palaemonetes pugio, Penaeus aztecus, Penaeus setiferus,* and *Callinectes sapidus,* and small fish, *Gobiosoma bosci, Lagodon rhomboides, Leiostomus xanthurus, Fundulus similis* and *Micropogonias undulatus.* Excluding residents *P. pugio, G. bosci* and *F. similis,* most of the macrofauna were transient juveniles of estuarine-dependent species. Among crustaceans, *P. pugio, P. aztecus,* and *C. sapidus* were significantly more dense in vegetated habitat, but *P. setiferus* was not consistently more abundant in either vegetated or nonvegetated habitat. Of 29 species of fishes, 14 were usually in vegetation, 11 were more often on nonvegetated bottom, and 5 were indifferent to either habitat.

Much seasonal variability in abundances of *P. aztecus, P. setiferus,* and *C. sapidus,* but not *P. pugio,* could be attributed to changes in temperature, salinity and water-level. Strong selection for vegetated habitat by *P. aztecus* was related to the historical water-level pattern coinciding with seasonal periods of marsh flooding. Apparently, high seasonal tides during the spring and fall facilitated access to vegetated habitat in the marsh and exploitation by transient *P. aztecus.* In contrast, strong selection for vegetation by *P. pugio,* abundant year-around in the marsh, was not similarly influenced by seasonal changes in water-level. Overall, habitat-related densities and physical interactions suggest that marsh physiography together with differences in tides may greatly determine the extent to which certain estuarine macrofauna utilize marsh habitats.

Introduction

The general importance of tidal marshes to estuarine dependent species has been recognized (Herke 1971; Turner 1977; Thayer et al. 1978; Weinstein 1979; Montague et al. 1981). However, utilization of marsh habitat by estuarine species has not been

well documented nor understood. Traditionally, reviews of salt-marsh animals, such as Daiber (1977 and 1982), have not incorporated treatment of transient species because Teal (1962) did not consider them to be important consumers in the marsh. In contrast, Bell and Coull (1978) and Bell (1980) have demonstrated that estuarine predators may have a significant impact on marsh meiofauna, and Montague et al. (1981) prepared a list of potentially impor-

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tant estuarine macroconsumers found in salt marshes. This suggests that marsh habitats may be exploited by natant estuarine macrofauna (Bell 1980) including the juveniles of transient species (Thayer et al. 1978; Weinstein 1979).

Estuarine macrofauna have access to marshes through drainage creeks and ponds, and density differences between adjacent vegetated and nonvegetated areas should reflect particular habitat selection or dependency. In seagrass communities, for example, certain macrofaunal abundances have coincided with the presence or absence of vegetation (Heck and Orth 1980; Stoner 1980; Lewis and Stoner 1983). As in seagrasses, estuarine species may temporarily utilize marsh habitat as cover against predation (Minello and Zimmerman 1983) or as a feeding ground (Bell 1980). In the past, the coarse physical nature of marsh vegetation has impaired sampling and comparison of abundances of natant estuarine species between marsh habitats (Zimmerman et al. 1984).

Although *Spartina* marshes predominate along Atlantic and Gulf of Mexico coastlines of temperate North America (Chapman 1960), their variable physiography (Steers 1977) and tidal regimes (Provost 1976) may greatly influence accessibility for estuarine macrofauna. Barren areas within marshes become established through pan formation (Yapp et al. 1917; Redfield 1972), due to devegetation by tidal wrack burial (Kurz and Wagner 1957; Reidenbaugh and Banta 1980), grazing and undermining by organisms (Lynch et al. 1947; Crichton 1960), vegetational rot (Chapman 1960), and erosion (Reidenbaugh et al. 1983). Differential patterns of accretion and erosion generally develop (Redfield 1972) and maintain (Reidenbaugh et al. 1983) nonvegetated areas as subtidal habitat and vegetated areas as intertidal habitat. Extensive nonvegetated bottom in salt marshes with connections to tidal creeks may increase macrofaunal access to vegetated habitat. Since tidal flooding expands the surface area of a marsh, the variable height and duration of tides (Provost 1976) will also affect marsh utility for estuarine species. In lower Galveston Bay marshes, nonvegetated bottom appears to be more extensive and interconnected (Zimmerman et al. 1984) than in At-

lantic coastal marshes (Teal 1962; Redfield 1972). In addition, the range of tides is smaller and seasonal flooding is more pronounced in the Gulf of Mexico than in the Atlantic (Provost 1976; Smith 1978; Hicks et al. 1983).

Our investigation has centered on establishing whether natant estuarine macrofauna utilize *Spartina alterniflora* habitat in a Texas salt marsh. Our approach was to compare macrofaunal densities from adjacent vegetated and nonvegetated habitats within the marsh. Since water-level fluctuations influence the accessibility of vegetation, macrofaunal densities were also examined relative to seasonal tide changes.

Methods

Site

The study was conducted in a salt marsh (29°12'N, 94°58'W) on the protected side of Galveston Island. Intertidal vegetation was predominately *S. alterniflora* and the adjacent subtidal bottom was without vegetation. Water depth was usually less than 1 m and the difference between intertidal and subtidal areas in the marsh averaged only 20 cm. Tides in the region are mixed, and the daily mean tidal range of 30 cm is dominated by 1 m seasonal excursions (Hicks et al. 1983). Vegetation occurred in patches varying in size between 1 to 25 m in width and 1 to 100 m in length. Nonvegetated bottom within the confines of the marsh occupied from 50 to 70% of the area. These non-vegetated pans, ponds, and creeks were of varying sizes and were interconnected through a reticulated network, opening into coves and bayous of a secondary bay. The marsh extended into the island for about 2.5 km, and drainage from terrestrial habitats was small. From the air, the site appeared to be ' similar to other marshes bounding the lower Galveston Bay system.

Study Design

The study was primarily designed to detect differences in densities of natant macrofauna between vegetated and nonvegetated areas in a *Spartina* marsh. Pairs of samples from adjacent vegetated and nonvegetated habitat formed the basic sampling units. The premise was that density differences between samples of each pair (within

pair comparison of habitats) reflected differential habitat utilization and inferred habitat selection. All samples were taken near respective habitat boundaries (within 3 m on both sides of the vegetated/nonvegetated edge). Density differences for crustaceans were evaluated separately for each monthly set of samples using a t-test of paired observations (Steel and Torrie 1960). The density relationship between habitats was further examined by computing selection as percentage in vegetation from the total in each sample pair. Within habitats, monthly densities were compared using ANOVA with Tukey's studentized range test (Steel and Torrie 1960).

Relationships between macrofaunal densities and physical-parameters were also examined. The selected physical variables were temperatures, salinity, and water-level. Pearson product-moment correlations and multiple linear regression models (RSQUARE Procedure) were computed with SAS Institute, Inc. (1982) algorithms using log-transformed densities. Correlations and regressions included data for the entire year, therefore seasonal variability provided the dominant effect. Similar comparisons were also made using physical factors and percentage in vegetation (arcsine transformed).

PROCEDURES

The samples were acquired using a drop sampler developed to give accurate and comparable estimates of macrofaunal densities in vegetated and nonvegetated habitat (Zimmerman et al. 1984). Samples were always taken in pairs, one in each habitat, and were generally less than 4 m apart. Each sample covered an area of 2.8 m², and 12 replicate pairs (12 per habitat) were obtained during each of 11 sampling periods (monthly sets). The interval between March 1982 and March 1983 was chosen for study in order to roughly incorporate one biological year for immigrating *P. aztecus* and *P. setiferus* (Baxter and Renfro 1967). Samples within each monthly set were acquired over an interval of 3 days during daylight within 2 hours of high tide.

In taking pairs of samples, a sampler was hoisted with a boom mounted on the bow of a skiff and quietly maneuvered over vegetated or nonvegetated bottom. The device was allowed to free-fall to the bottom and then disconnected. Immediately following, the operation was repeated with a second sampler over the other habitat. The habitat sequence was reversed from pair to pair, and special care was taken not to disturb the site until the second sampler was deployed. The cylindrical samplers (1.8 m diam. × 1.2 m ht) were pushed at least 15 cm into the substrate. Water from each sampler was pumped into a 1 mm mesh plankton net and the enclosed bottom was thoroughly swept with dip nets after vegetation was removed. All sample contents were washed into the plankton net cod-end bag which was removed and transferred to formalin with Rose Bengal stain for laboratory processing. Tide levels were measured in the marsh and calibrated against data provided by the National Oceanic and Atmospheric Administration/National Ocean Survey (NOAA/NOS, Rockville, Maryland 20852) for Station No. 8771450 at Pier 21, Galveston, Texas. Historical annual water-level variation for the station (1908 to 1980) was taken from Hicks et al. (1983). Salinity, water depth, tidal height, water temperature, and dissolved oxygen were measured with each sample. Continuously recording thermographs, one each in vegetated and nonvegetated areas, provided additional data.

In the laboratory, natant macrofauna consisting of fishes and crustaceans above 10 mm in length were removed from each sample, measured, and counted. Meiofaunal species with some individuals exceeding 10 mm, such as amphipods, were not effectively sampled and were not included in the data.

Results

PHYSICAL CHARACTERISTICS OF THE MARSH

Many physical characteristics of the Galveston marsh site were discussed by Zimmerman et al. (1984). The dominating physiographic feature was extensive reticulation created between *S. alterniflora* and nonvegetated habitat. Water depth was abruptly different between habitats at their common edge (x̄ difference = 19.7 cm), but temperature, salinity, and dissolved oxygen did not differ (Zimmerman et al. 1984). Monthly temperature and salinity values
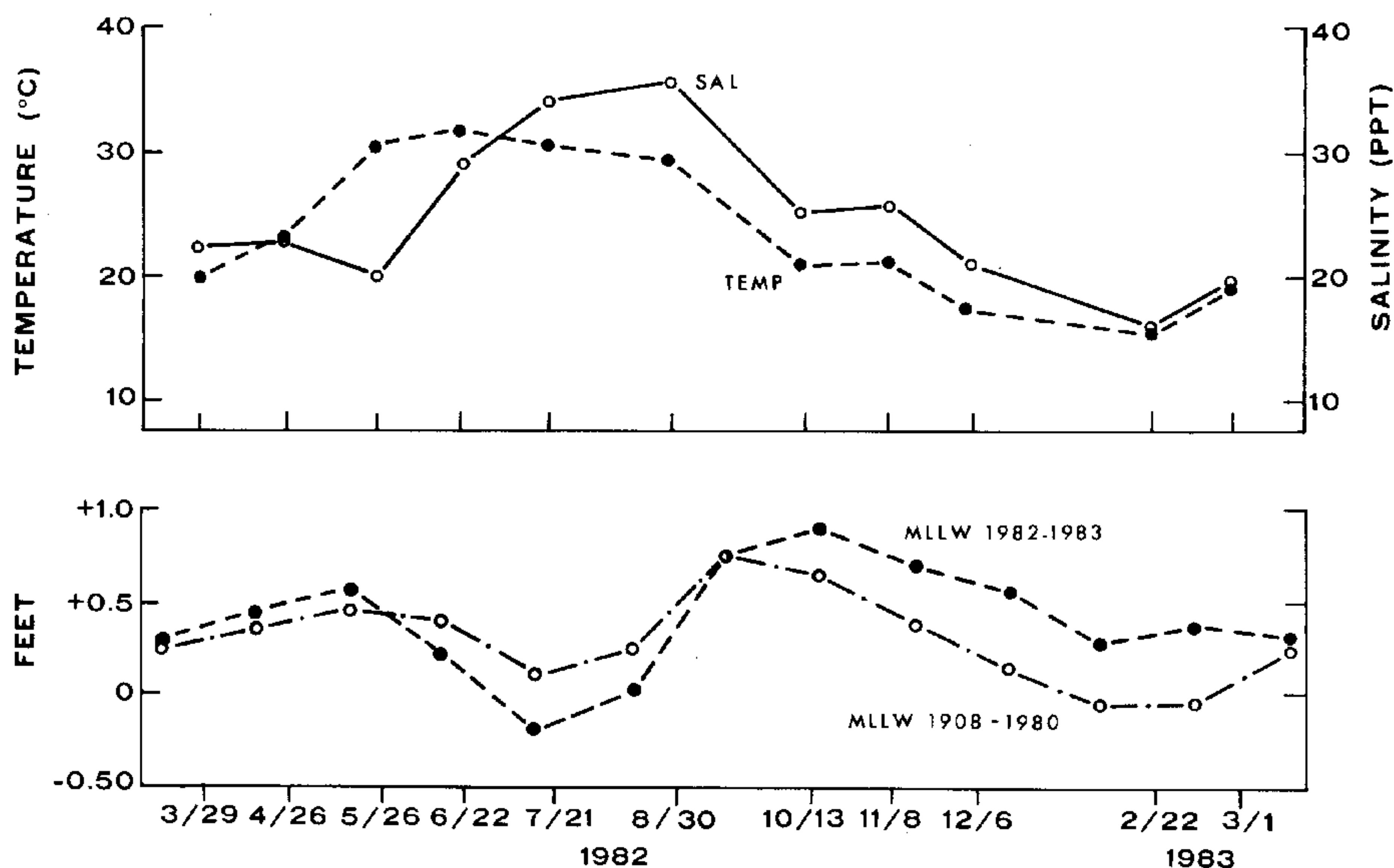
Fig. 1. Mean temperature, salinity and water-level excursions in a Galveston Bay salt marsh. The tidal reference (0) is mean lowest low water (MLLW).

were positively correlated (r = +0.71, p < 0.01), and mid-day means ranged from 15.2 to 31.7 °C and 16.0 to 36.0‰ (Fig. 1). Historically, tidal water-levels in Galveston Bay are highest during the spring and fall and lowest during the winter and summer (Hicks et al. 1983). Water-level in 1982–83 was roughly similar to the historical pattern (Fig. 1), but varied enough so that respective monthly means were not significantly correlated (r = +0.52, p = 0.10). During the summer of 1982 water was higher and in the winter of 1983 lower than historical levels. Importantly, seasonal density patterns of some species were more closely related to historical than actual water-level.

SPECIES—HABITAT RELATIONSHIPS

Densities of the crustaceans *Palaemonetes pugio*, *Penaeus aztecus* and *Callinectes sapidus* were significantly higher in vegetated compared to nonvegetated habitat, whereas *Penaeus setiferus* densities were not different (Fig. 2, Table 1). In vegetation, summer densities of *P. pugio* were highest (70 per m²), and winter densities of *P. aztecus* (0.1 per m²) and *P. setiferus* (0) were

lowest. On nonvegetated bottom, summer densities of *P. setiferus* (12 per m²), were highest and summer densities of *P. pugio* (0.1 per m²) were lowest. All species, except *P. setiferus*, were present in the marsh throughout the year (Table 1) and *P. pugio* and *C. sapidus* were always more numerous in vegetated habitat. *Penaeus setiferus* and *P. aztecus* were occasionally more abundant on nonvegetated bottom. Percent abundance in vegetation (potential habitat selection) within the areas sampled was, from highest to lowest, *P. pugio*, *C. sapidus*, *P. aztecus*, and *P. setiferus* (Fig. 3). *Palaemonetes pugio* and *C. sapidus* always appeared to select for vegetation. On the other hand, vegetational selection by *P. aztecus* appeared to be seasonal and *Penaeus setiferus* did not select either habitat over the other. Size-frequencies of the macrocrustaceans sampled confirmed that all except *P. pugio* were juvenile populations (Fig. 4).

Overall fish abundance was highest on vegetated bottom but individual species exhibited differences in habitat selection (Table 2). Unfortunately, low numbers for most fish species precluded use of the paired *t*-
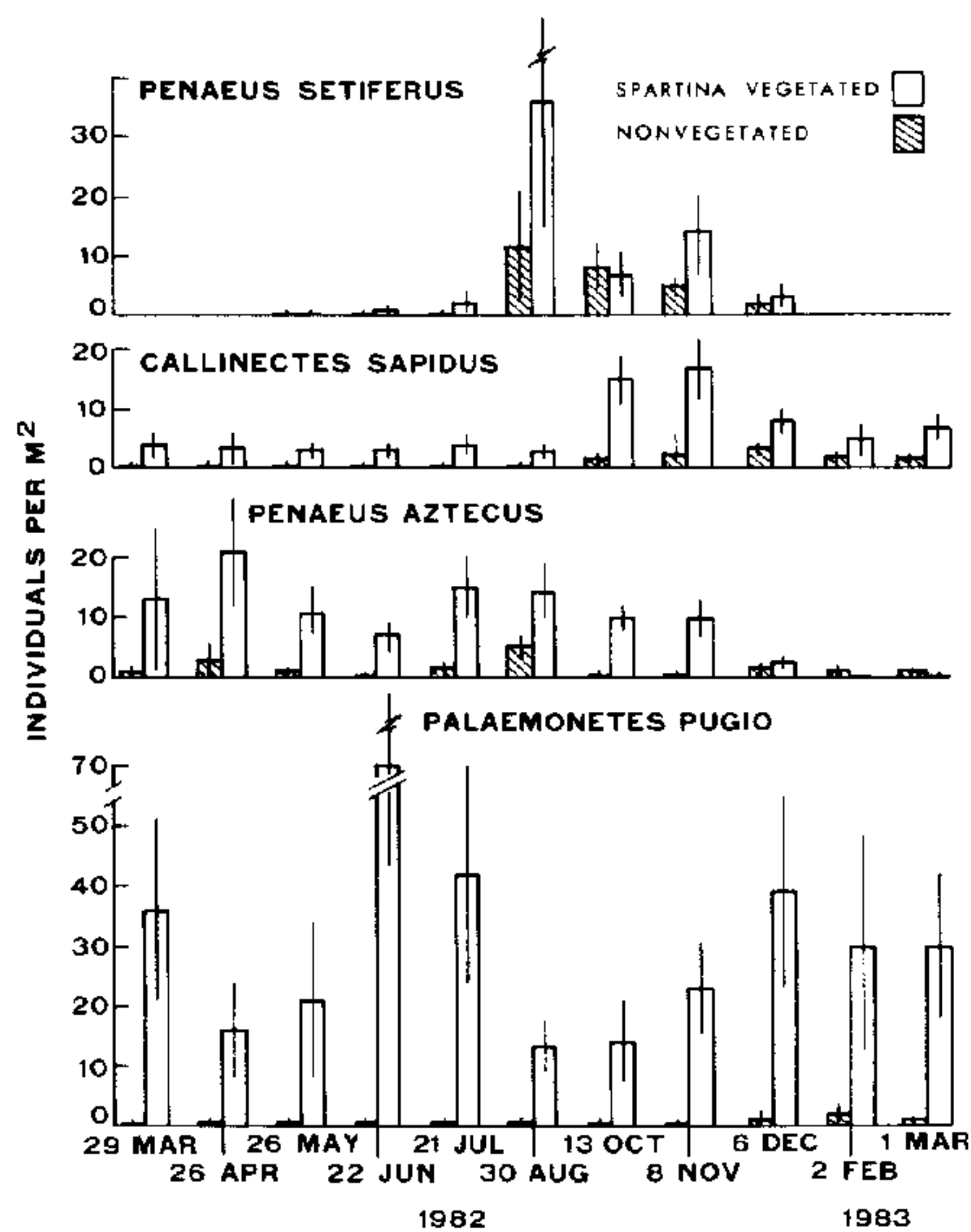
Fig. 2. Comparative densities (mean and 95% C.I., untransformed data) of macrocrustaceans from *Spartina alterniflora* habitat and adjacent nonvegetated habitat in a Galveston Bay salt marsh.
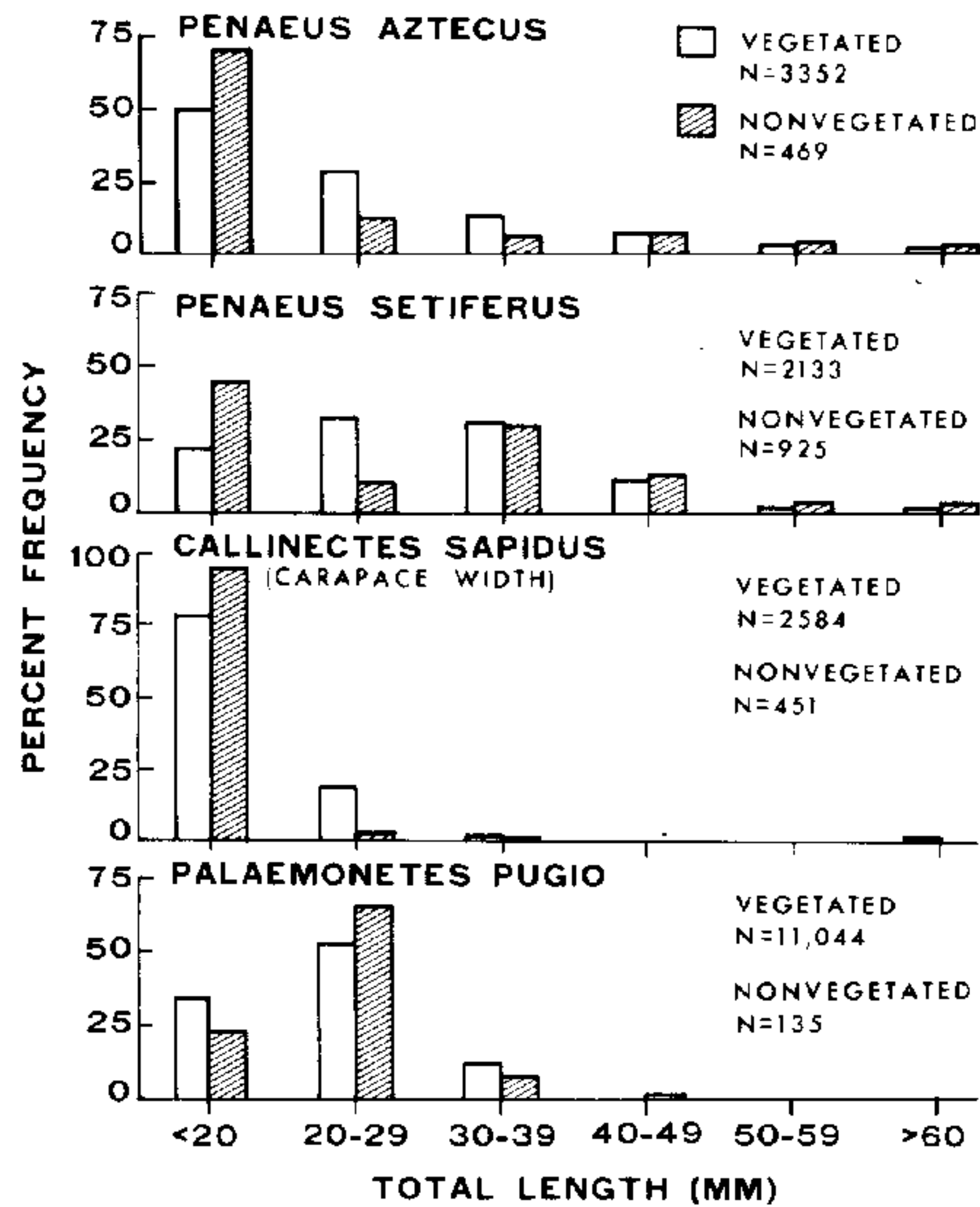

Fig. 4. Size-frequency distributions of macrocrustaceans from adjacent vegetated and nonvegetated habitats in a Galveston Bay salt marsh sampled between March 1982 and March 1983.

test and made most other statistical tests impractical. However, among 29 species collected, 14 species each had 75% of their abundance in vegetated habitat and 10 species had 75% of their abundance in nonvegetated habitat. Only 5 species showed no
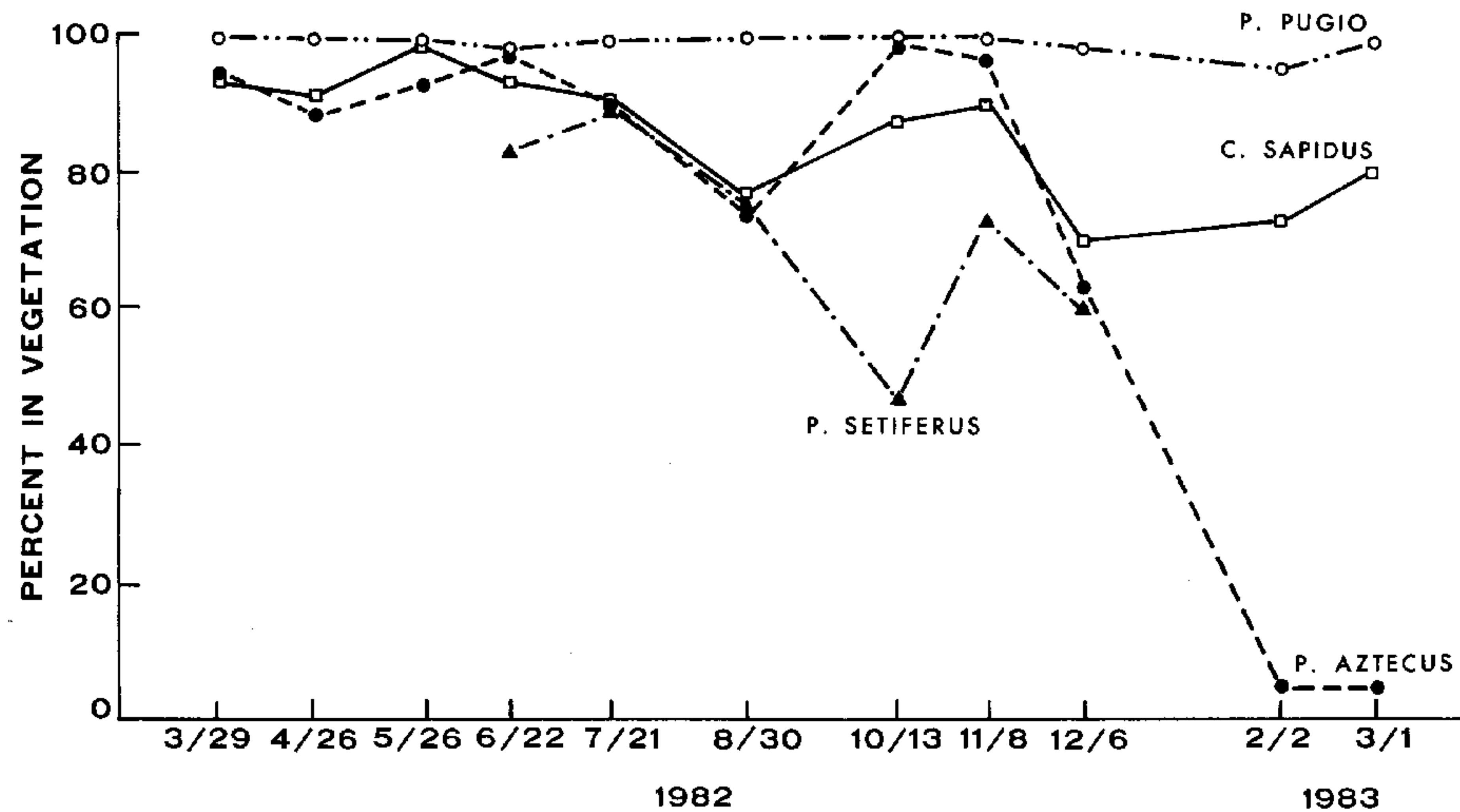

Fig. 3. Percent abundance of macrocrustaceans in *Spartina alterniflora* habitat versus adjacent nonvegetated habitat compared on an equivalent area basis in a Galveston Bay salt marsh.

TABLE 1. Mean densities (number per m^2) of crustaceans in vegetated and nonvegetated habitats in a Galveston Bay salt marsh.

Date	Penaeus aztecus Veg/Nonveg	Penaeus setiferus Veg/Nonveg	Palaemonetes pugio Veg/Nonveg	Callinectus sapidus Veg/Nonveg
03/29/82	13.3/0.8*	0/0	35.8/0.1***	4.1/0.3***
04/26/82	21.1/2.8**	0/0	15.9/0.2***	3.5/0.3***
05/26/82	10.6/1.0***	0.2/0***	21.0/0.1***	2.6/0.1***
06/22/82	6.8/0.2***	0.6/0.1 n.s.	69.9/0.2***	2.9/0.2***
07/21/82	15.0/1.6***	2.0/0.2 n.s.	43.1/0.1***	3.9/0.4***
08/30/82	14.4/5.0***	36.3/12.1 n.s.	13.3/0***	2.8/0.8*
10/13/82	9.9/0.1**	6.8/7.8 n.s.	14.0/0.1***	15.0/1.9***
11/08/82	9.6/0.4***	14.3/5.2*	23.1/0.1***	22.3/2.4***
12/06/82	2.3/1.3**	3.3/2.1 n.s.	39.4/0.7***	8.2/3.5**
02/02/83	0.1/0.5*	0/0	29.7/1.7***	5.1/1.9*
03/01/83	0.1/0.5*	0/0	30.3/0.4***	7.3/1.8***

Paired t-test (Steel and Torrie 1960) performed on samples in each set (each date) for each species, n = 12 pair/set; * p < 0.05, ** p < 0.01, *** p < 0.001.

selection for either habitat. Among the six most abundant fishes (82% of total abundance), *Gobiosoma bosci*, *Lagodon rhomboides* and *Fundulus similis* selected for vegetation, while *Leiostomus xanthurus* and *Anchoa mitchilli* selected nonvegetated bottom and *Micropogonias undulatus* was indifferent to either habitat.

DENSITY RELATIONSHIPS AMONG SPECIES

Within Habitats

On an annual basis, the order from high to low density in vegetation was *P. pugio*, *P. aztecus*, *C. sapidus*, and *P. setiferus* for crustaceans, and *G. bosci*, *L. rhomboides*, *F. similis*, *Cyprinodon variegatus*, and *Cynoscion nebulosus* for fish. Monthly density means in vegetation were significantly higher for *P. pugio* and lower for *P. setiferus* during the year compared with other crustaceans (ANOVA, Tukey's test, p < 0.05). In vegetated habitat, density correlations (p < 0.01, n = 129) were significant between *C. sapidus* and fish (r = +0.43), *C. sapidus* and *P. setiferus* (r = +0.32), and *P. aztecus* and *P. setiferus* (r = +0.28). The lack of correlation between *P. pugio* and any other species emphasizes the difference of its seasonal density pattern.

Rank order from high to low density in nonvegetated habitat was *P. setiferus*, *P. aztecus*, *C. sapidus*, and *P. pugio* for crustaceans, and *L. xanthurus*, *A. mitchilli* and *Brevoortia patronus* for fish. Mean densities by month during the year on nonvegetated bottom were significantly lower for *P. pugio*

compared with other crustacean species. Significant (p < 0.01, n = 129) correlations in densities over time within nonvegetated habitat were between *C. sapidus* and *P. setiferus* (r = +0.34), and *C. sapidus* and *P. pugio* (r = +0.32). The pattern of densities for *P. aztecus* over time was not similar to other species on nonvegetated bottom.

Between Habitats

Habitat selection (percent abundance in vegetation) was compared among species. Strong selection for vegetated habitat by *P. pugio* was correlated with selection by each of the other crustaceans (p < 0.01). Vegetational selection between *P. aztecus* and *C. sapidus* was also significantly correlated at the 0.01 level (r = +0.42). Using selection as an indicator, the order of strength of association with vegetated habitat was *P. pugio*, *C. sapidus*, *P. aztecus*, and *P. setiferus*. Lack of significant selection by *P. setiferus* suggested indifference toward either habitat. Except for *P. aztecus* during winter months, significant selection for nonvegetated habitat was not observed.

RELATIONSHIPS TO PHYSICAL FACTORS

In vegetated habitat, combined seasonal variability of temperature/salinity/1982–83 water-level could account for as much as 58%, 55%, and 44% of density changes in *P. setiferus*, *P. aztecus*, and *C. sapidus*, respectively, but only 9% in *P. pugio* (Table 3). Seasonal relationships of *P. aztecus* densities and temperature, salinity, and histor-

TABLE 2.   Seasonality in densities of fish (individuals per 10 m²) in vegetated (V) and nonvegetated (NV) habitats within a Galveston Bay salt marsh.

Species	29 Mar. V/NV	26 Apr. V/NV	26 May V/NV	22 June V/NV	21 July V/NV	30 Aug. V/NV	13 Oct. V/NV	8 Nov. V/NV	6 Dec. V/NV	2 Feb. V/NV	1 Mar. V/NV	Total No. Indi- viduals	Mean % in Veg.[1]
Gobiosoma bosci	0.6/0	0.4/0	0.5/0.1	1.9/0.6	1/0	3/0.6	24.8/6.2	21.8/4.2	3.6/2.4	0	1.5/1.5	482	(81)
Lagodon rhomboides	16/0	6.7/2.3	3.7/1.4	1.5/1.5	0.5/0.5	1.8/0.4	0	0	0	0	2.7/0.1	378	(76)
Leiostomus xanthurus	5/5	0.9/5.1	0.9/3.1	0/0.7	0/0.3	0	0.3/0.4	0/0.3	0	0/0.6	0.1/9.9	112	(15)
Anchoa mitchilli	0	0	0/0.3	0/1.8	0/0.3	0/0.4	0.3/3.3	2.8/7.2	0/0.1	0	0	109	(5)
Fundulus similis	1.5/0	0	0.1/0	0.9/0	0.9/0	0.8/0	0	3/0	2/0	0.3/0	0	62	(100)
Micropogonias undulatus	1.2/0.2	0/0.9	0.3/0.1	0	0	0	0.3/0.1	0/0.8	0	3.2/4.8	0	54	(43)
Brevoortia patronus	1.4/0.2	0.4/0.9	0/0.1	0/0.6	1.4/5.6	0.3/2.2	0	0	0/0.1	0/0.1	0/0.1	36	(19)
Cyprinodon variegatus	2.4/1	0	0	0.6/0	0.3/0	0.7/0	0	0.6/0	0.5/0	0	0	35	(95)
Cynoscion nebulosus	0	0	0	0.5/0.2	0.9/0	0.7/0	0.4/0.2	1.7/0.1	0.3/0	0	0	34	(91)
Paralicthys lethostigma	0.4/0	0.9/0.4	0.4/0.3	0.5/0.2	0	0	0/0.3	0/0.1	0	0	0.5/0.2	28	(55)
Mugil cephalus	0.8/0.2	0/0.1	0/0.3	0.5/0.2	1.4/5.6	1.5/1.5	0	0	0	0/0.1	0	21	(33)
Menidia beryllina	0/0.2	0	0	0.2/0.5	1.4/5.6	0/0.4	0/0.4	1.5/1.5	0	0	0/0.1	19	(14)
Fundulus grandis	0	0.1/0	0.1/0	0.3/0	0.3/0	0	0	0.7/0	0	0	0.7/0	14	(100)
Sciaenops ocellatus	0	0	0.1/0	0	0	0	0	0	1.2/0.4	0.1/0	0	13	(91)
Symphurus plagiusa	0/0.1	0	0/0.1	0/0.1	0	0/0.3	0.2/0.4	0.1/0	0	0	0/0.1	11	(18)
Myrophis punctatus	0	0	0/0.1	0.2/0.5	0	0/0.1	0.1/0	0/0.1	0	0	0	8	(25)
Microgobius thalassinus	0	0	0	0	0	0	0/0.1	0/0.3	0	0/0.4	0/0.1	7	(0)
Citharicthys spilopterus	0	0/0.3	0/0.4	0	0	0	0	0	0	0	0	5	(0)
Achirus lineatus	0	0	0	0	0	0.6/0	0.1/0	0	0	0	0	5	(100)
Gobionellus boleosoma	0	0.1/0	0	0	0	0	0	0	0	0.1/0.3	0	4	(67)
Synodus foetens	0	0	0/0.4	0	0	0	0	0	0	0	0	3	(0)
Lucania parva	0.4/0	0	0	0	0	0	0.1/0	0	0	0	0	3	(100)
Elops saurus	0.2/0.2	0	0	0	0	0	0	0	0	0	0	2	(50)
Syngnathus sp.	0	0	0.3/0	0	0	0	0	0	0	0	0	2	(100)
Pogonias cromis	0	0	0	0	0	0.1/0	0	0	0	0	0	1	(100)
Orthopristis chrysoptera	0	0	0.1/0	0	0	0	0	0	0	0	0	1	(100)
Microgobius gulosus	0	0	0	0.1/0	0	0	0	0	0	0	0	1	(100)
Opsanus beta	0	0	0	0	0	0	0.1/0	0	0	0	0	1	(100)
Membras martinica	0	0	0	0	0	0	0	0	0/0.1	0	0	1	(0)

[1] Mean percent in vegetation was calculated on a monthly basis.

TABLE 3. Multiple regression models[1] for crustacean densities versus selected physical variables in a Galveston Bay salt marsh.

Independent Variables	Dependent Variables			
	Penaeus aztecus	Penaeus setiferus	Calli- nectes sapidus	Palaeo- monetes pugio
Vegetated habitat:				
[2]MLWH	0.342	0.046	0.017	0.030
[3]MLW82	0.002	0.063	0.318	0.085
[4]Temp	0.354	0.020	0.197	0.005
[5]Sal	0.327	0.287	0.020	0.002
Temp-MLW82	0.493	0.153	0.356	0.092
Temp-MLWH	0.486	0.049	0.327	0.056
Temp-Sal	0.398	0.406	0.260	0.005
Sal-MLW82	0.411	0.542	0.326	0.091
Sal-MLWH	0.544	0.296	0.048	0.037
Temp-Sal-MLW82	0.551	0.582	0.439	0.093
Temp-Sal-MLWH	0.552	0.470	0.417	0.058
Nonvegetated habitat:				
[2]MLWH	0.015	0.094	0.054	0.111
[3]MLW82	0.057	0.178	0.145	0.007
[4]Temp	0.063	0.001	0.329	0.070
[5]Sal	0.131	0.169	0.054	0.084
Temp-MLW82	0.081	0.241	0.344	0.129
Temp-MLWH	0.128	0.111	0.330	0.130
Temp-Sal	0.131	0.326	0.393	0.091
Sal-MLW82	0.142	0.575	0.153	0.131
Sal-MLWH	0.176	0.218	0.088	0.160
Temp-Sal-MLW82	0.144	0.618	0.413	0.132
Temp-Sal-MLWH	0.182	0.492	0.395	0.160

[1] The entries are linear regression values (R^2) computed for each species (dependent variables) against single and combined physical factors (independent variables) using a program by SAS Institute, Inc. (1982).
[2] Mean lowest low water 1908–80 (Historical).
[3] Mean lowest low water 1982–83.
[4] Temperature.
[5] Salinity.

TABLE 4. Multiple regression model[1] for selection of vegetation by crustaceans versus selected physical variables in a Galveston Bay salt marsh.

Independent Variables	Dependent Variables			
	Penaeus aztecus	Penaeus setiferus	Calli- nectes sapidus	Palaeo- monetes pugio
[2]MLWH	0.491	0.015	0.156	0.110
[3]LMW82	0.050	0.085	0.001	0.003
[4]Temp	0.180	0.078	0.157	0.092
[5]Sal	0.130	0.008	0.11	0.108
Temp-MLW82	0.475	0.091	0.193	0.143
Temp-MLWHW	0.527	0.090	0.219	0.142
Temp-Sal	0.189	0.128	0.222	0.118
Sal-MLW82	0.320	0.109	0.011	0.148
Sal-MLWH	0.570	0.020	0.156	0.178
Temp-Sal-MLW82	0.506	0.151	0.251	0.176
Temp-Sal-MLWH	0.570	0.160	0.270	0.178

[1] The entries are linear regression values (R^2) computed for each species (dependent variables) against single and combined physical factors (independent variables) using a program by SAS Institute, Inc. (1982).
[2] Mean lowest low water 1908–80 (Historical).
[3] Mean lowest low water 1982–83.
[4] Temperature.
[5] Salinity.

ical water-level were each similar, and the latter explained more variability than 1982–83 water-level changes. The best pairwise combination for *P. aztecus* in vegetation was salinity/historical water-level. For seasonal abundance of *P. setiferus* in vegetation, salinity as a single factor and in combination with the 1982–83 water-level accounted for most variability (Table 3). Seasonal changes in *C. sapidus* were most related to 1982–83 water-level separately and in combination with temperature (Table 3). Variability in *P. pugio* was not related to variation in physical factors.

On nonvegetated bottom, combined seasonal variability of temperature/salinity/ 1982–83 water-level accounted for 62% and

41% of seasonal variation in *P. setiferus* and *C. sapidus*, respectively, but only 14% and 13% in *P. aztecus* and *P. pugio*, respectively (Table 3). As in vegetated habitat, densities of *P. setiferus* on nonvegetated bottom were related to seasonal salinity and 1982–83 water-level variations. For *C. sapidus* in nonvegetated habitat, seasonal abundances were more related to temperature and temperature/salinity variations (Table 3). Seasonal variability in densities of *P. aztecus* and *P. pugio* in nonvegetated habitat could not be attributed to any combination of physical variables.

Variability in habitat selection was only well explained in *P. aztecus* and only by seasonal pattern of historical water-level (Table 4).

Discussion

The dominance of macrocrustaceans *P. pugio, P. aztecus, P. setiferus* and *C. sapidus* in the proximity of the study site was described by Trent et al. (1976). The commercial species *P. aztecus, P. setiferus* and *C. sapidus* are estuarine-dependent as juveniles (Williams 1965) and *P. pugio* is an estuarine resident commonly associated with marsh habitats (Wood 1967). Utili-

zation of marsh (*S. alterniflora* habitat) by these and other natant macrofauna has been implied (Bell 1980) but abundances within vegetation have not been previously known. Since these are essentially aquatic estuarine species, their periodic movement into intertidal marsh could be of substantial importance by adding habitat for their own feeding and cover, and by impacting other populations. However accessibility and potential utility of marsh to estuarine species may be highly dependent upon physiography and tidal regimes. Since these features vary regionally (Provost 1976), some marshes may provide greater opportunity for exploitation than others.

Some natant estuarine macrofauna may have become more or less dependent upon exploitation of vegetated habitat within marshes. Species such as *P. pugio* (Welsh 1975; Morgan 1980) and *Fundulus heteroclitus* (Kneib and Stiven 1982) have been shown to directly depend upon vegetated habitat and are cited as reference for comparison. By contrasting adjacent vegetated and nonvegetated densities of species in marshes under equivalent conditions, potential habitat selection or dependency can be measured. In our study, densities were measured at flood tide when vegetated and nonvegetated habitats were equally available. At low tide when vegetated habitat had drained, all natant species including *P. pugio* and *Fundulus* spp. moved onto nonvegetated bottom comprised of small intertidal pools, subtidal ponds, and creeks.

The grass shrimp, *P. pugio*, was abundant in vegetated habitat throughout the year (Fig. 2, Table 1). On nonvegetated bottom, densities were among the lowest for crustaceans and provided strong evidence supporting selection of vegetated habitat. The apparent attraction may be related to protection (Coen et al. 1981), and feeding (Morgan 1980). The comparatively poor relationship between densities of *P. pugio* and temperature, salinity, and water-level (Table 3) confirmed the broad tolerance range cited for this species (Wood 1967; Welsh 1975; Thorp and Hoss 1975). Major summer (July) and minor winter (December) density peaks reflected recruitment from spring and fall reproductive periods (Wood 1967).

During late March through November,

juvenile brown shrimp (*P. aztecus*) were abundant in the marsh (Fig. 2, Table 1) and significantly more abundant in vegetated compared with nonvegetated habitat. From December through mid-March, *P. aztecus* was present only in low densities and did not select for vegetated habitat. Beginning about the vernal equinox (Fig. 2) and depending upon late winter and early spring onshore Ekman transport (Saila et al. 1982), brown shrimp postlarvae immigrate into the estuary in large numbers (Baxter and Renfro 1967) and migrate to the marshes (Parker 1970). Historically, water-levels in Gulf of Mexico estuaries are highest in the spring and fall (Hicks et al. 1983). As a consequence, intertidal vegetation is more available for longer periods to juvenile shrimp and other organisms during these intervals. Under usual spring and fall conditions, densities of brown shrimp are highest and growth is about 1.1 mm per day (Knudsen et al. 1977, for review). Brown shrimp leave the marsh at 50 to 60 mm (Fig. 4). Juveniles smaller than 50 mm are rarely found in the open estuary and emigration to offshore occurs at sizes ranging between 58 to 98 mm (Trent 1967). It appears that juvenile brown shrimp may spend most of their early residence in or near marsh habitat. As a consequence, production and survival of postlarval and early juvenile brown shrimp may be partially related to availability of optimal marsh conditions. We propose that exploitation of vegetated habitat may improve crucial estuarine nursery functions, and that the quality of intertidal *Spartina* habitat and the interaction of water-level may greatly determine the utility of a marsh for brown shrimp.

White shrimp (*P. setiferus*) were highly seasonal within the marsh and densities were not significantly different between vegetated and nonvegetated habitat. High densities were present from August through November, and low densities occurred from May through July and in December (Fig. 2, Table 1). From January through April, *P. setiferus* was essentially absent from the marsh. Postlarvae apparently enter the estuary during the late spring and summer (Baxter and Renfro 1967) as warm season recruits (Holt and Strawn 1983). Habitat-related distribution has not been well defined, but ju-

veniles have been generally associated with nonvegetated bottom (Loesch 1965; Stokes 1974). Our data suggest that juvenile white shrimp may utilize marsh vegetation and adjacent nonvegetated bottom on an equivalent basis when available and may respond to different factors than brown shrimp. In addition, some degree of competitive interaction may take place between the species. Giles and Zamora (1973) demonstrated in the laboratory that displacement of *P. setiferus* from vegetation onto nonvegetated bottom by *P. aztecus* may be possible, although experimental densities were unnaturally high. In our study, the species occupied the marsh at peak abundances during different periods, but occasional selection for vegetation by white shrimp was unrelated to absence of brown shrimp (Fig. 2). White shrimp also emigrate from the bay at a larger size ($\bar{x} = 99$ mm, range of means = 86 to 146 mm) than brown shrimp (Pullen and Trent 1969) suggesting a longer residence period.

Blue crabs *C. sapidus* were present in the marsh throughout the year (Fig. 2). Selection for vegetated compared with nonvegetated bottom was always significant (Table 1). The life cycle of *C. sapidus*, as a resident estuarine species (Darnell 1959; Hammerschmidt 1982) with reproduction limited to higher salinities (Sandoz and Rogers 1944) and juveniles distributed over a range of conditions from brackish-water creeks (Daud 1979) to saline open-water sounds (Dudley and Judy 1973) has been described. Specific relationships with vegetated habitat have not been determined, but Harris (1982) attributes the decline in the Chesapeake bay blue crabs to loss of seagrass (*Zostera*) habitat and Lynne (1982) has attempted to infer economic value of Florida marsh partially based on a blue crab fishery. Our data have established that vegetated marsh may be preferred by early juveniles when available. The marsh population was mostly comprised of juveniles smaller than 40 mm in carapace width (Fig. 4). Adults were also present but densities were too low to establish habitat-related distributions.

Fish species were marginally more numerous within vegetation (Table 2) with 14 species selecting vegetated habitat and 10 species mostly in nonvegetated habitat. The

species *G. bosci*, *L. rhomboides*, and *F. similis* accounted for 89% of fish abundance in vegetation. On nonvegetated bottom, *A. mitchilli* and *L. xanthurus* comprised 71% of fish abundance for that habitat. The croaker *M. undulatus* was abundant overall but did not select for either habitat type. In other marshes *L. xanthurus*, *A. mitchilli*, *M. undulatus*, and *L. rhomboides* were among numerical dominants reported by Weinstein (1979) and Wenner et al. (1982). The goby *G. bosci* has been reported to be numerically dominant in ichthyoplankton of Cheapeake Bay (Shenker et al. 1983). Each of these fishes have been reported in temperate seagrass (*Zostera*) communities (Adams 1976; Orth and Heck 1980) and the distributions of *G. bosci* and *L. rhomboides* in seagrasses agree with our observations of vegetated habitat selection. Attraction to seagrasses by *L. xanthurus* and *A. mitchilli* (Orth and Heck 1980), however, was dissimilar compared to selection for nonvegetated habitat in our data (Table 2). These results lead us to conclude that seagrass and marsh habitats (vegetation *per se*) are not necessarily equivalent for all species. Differences in vegetational density, structure, and associated biota or differences in factors unrelated to vegetation may determine habitat selection.

Water-level was the single most important factor in regression models for *P. aztecus* densities in the marsh, thus supporting our contention that early juveniles of brown shrimp may specialize in exploiting vegetated habitat. As a consequence, the success of recruits in a marsh system may partially depend upon circumstances surrounding intertidal flooding such as the timing and range of daily and seasonal tides. If daily amplitude is low relative to seasonal tides, useful access to intertidal habitat may be seasonally periodic (Provost 1976). Such conditions exist in the Gulf of Mexico, where daily amplitude is about 30 cm and seasonal range is about 1 m (Hicks et al. 1983). The relatively high seasonal range, compared with daily range, provides higher tides and greater marsh inundation during the spring and fall (Fig. 1). The opposite effect occurs during the winter and to a lesser extent in the summer. In concert with equinox tides, major pulses of postlarval brown shrimp

immigrate into the estuarine system during the spring and again in the fall (Baxter and Renfro 1967). The percentage of *P. aztecus* in vegetation compared with adjacent non-vegetated bottom was also highest during these periods (Fig. 2). Perhaps as a mechanism protecting against less favorable circumstances, selection for vegetation diminishes during the summer and winter when seasonal tides are low. During the winter and to a lesser extent during the summer, brown shrimp were relatively abudant on subtidal nonvegetated bottom even when intertidal vegetation was flooded. In addition, summer densities of brown shrimp during seasonally low water were lower than the spring and fall density peaks corresponding to seasonally high water.

A single immigration pulse of *P. setiferus* postlarvae and highest abundance coincided with high salinities and temperatures and low summer water-levels. Tidal circumstances during the summer limited the availability and suitability of intertidal *Spartina* vegetation and provided evidence that juvenile white shrimp may exploit subtidal nonvegetated habitat better than brown shrimp. In support, Wheeler (1968) demonstrated in nonvegetated ponds that growth rates of postlarval *P. setiferus* (2.3 mm per day) exceeded those of postlarval *P. aztecus* (0.98 mm per day). Salinity may also be a habitat factor since white shrimp are customarily associated with lower salinities (Keiser and Aldrich 1976; Perry 1981). However, both white and brown shrimp can tolerate broad salinity ranges (Barrett and Gillespie 1973; Wiesepape 1975) and white shrimp have been found naturally in salinities as high as 41‰ (Gunter 1961). In our investigation, summer salinities were unusually high compared to other years surveyed (Pullen et al. 1971), but white shrimp abundances appeared unaffected. For instance, white shrimp during August were as dense as 103 per m² in samples having mid-day temperatures of 32 °C and salinities near 37‰.

In summary, the resident *P. pugio* was abundant in vegetation throughout the year and seasonal densities were not related to the physical parameters examined. Densities of other natant macrocrustaceans (transient juveniles) were seasonal, and much of their variability could be attributed to seasonal changes in salinity, temperature, and/or water-level. For *P. setiferus*, densities were primarily explained by wet-dry seasons corresponding to winter-summer changes. White shrimp densities did not differ significantly between vegetated and nonvegetated habitat. Variability in *C. sapidus* was mostly related to seasonal changes in temperature. Blue crabs were significantly more abundant in vegetation than on nonvegetated bottom. Water-levels provided the best correlation for explaining variation in seasonal densities of *P. aztecus*. Brown shrimp selected for vegetation during all except winter months. As a consequence, the physical characteristics of salt marshes and tidal interactions may be particularly important to brown shrimp and other estuarine species whose strategy includes direct exploitation of vegetated habitat.

ACKNOWLEDGMENTS

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